Postcocooning Temperatures and Diapause in the Alfalfa Pollinator *Megachile rotundata* (Hymenoptera: Megachilidae)

W. P. KEMP AND J. BOSCH

Bee Biology and Systematics Laboratory, USDA–ARS, Utah State University, Logan, UT 84322–5310

ABSTRACT *Megachile rotundata* (F.), an adventive, gregarious, cavity-nesting, leaf cutting bee, is used throughout North America for the pollination of alfalfa, *Medicago sativa* L., seed crops. We examined the influence of various postcocooning (prewintering) temperature regimes on development, survival, emergence time, and longevity in both nondiapausing and diapausing forms of this species. Diapausing male and female *M. rotundata* required 27–30 d and 29–32 d, respectively, to develop from prepupae to emergence after incubation at constant 29°C, regardless of postcocooning treatments to which they were exposed. Likewise, longevity after emergence was not related to postcocooning temperatures and ranged from 5 to 6 d and 4 to 6 d for males and females, respectively. Elevated postcocooning temperatures were associated with a higher prevalence of nondiapausing individuals, those completing development from eggs through emergence as adults in the same summer season. Relevance of our results to the commercial production of alfalfa leafcutting bees is discussed.

KEY WORDS alfalfa leafcutting bee, *Megachile rotundata*, development, emergence, mortality, pollination

THE ALFALFA LEAFCUTTING bee, *Megachile rotundata* (F.), is an adventive, gregarious, cavity-nesting, leaf-cutting bee that has been cultured extensively as a superior pollinator of alfalfa, following the first North American record of its presence in 1947 (Krombein 1948). Because of the widely appreciated contributions that this species makes to alfalfa seed, *Medicago sativa* L., production, much emphasis has been placed on developing wintering procedures and improved incubation schedules to synchronize the emergence of *M. rotundata* with alfalfa bloom (Stephen and Osgood 1965, Krunic and Hinks 1972, Rank and Goerzen 1982, Richards et al. 1987, Richards and Whitfield 1988, Murrell 1991, Peterson et al. 1992). At the same time, the body of literature on which we rely for insights into the summertime temperature-dependent development of *M. rotundata* is comparatively small (Taséi and Masure 1978, Undurraga 1978, Whitfield and Richards 1992, Kemp and Bosch 2000).

At most North American latitudes, *M. rotundata* emerge and mate during June and July, and female bees build their nests in pre-established cavities such as beetle burrows in trees along river courses, in cavities associated with farm buildings, or artificial nesting materials provided by alfalfa seed producers (Stephen 1981, Rank and Goerzen 1982, Richards 1984). Nesting continues for 4–6 wk and nests consist of a linear series of cells constructed from cut-leaf pieces. Each cell is provisioned with a mass of pollen and nectar, on top of which an egg is deposited. Completed nests are sealed with cut-leaf plugs. *M. rotundata* is a polylectic species, but females are strongly attracted to flowers of several legume genera, including *Medicago* and *Melilotus*.

By midsummer, fifth-instar *M. rotundata* complete the consumption of their pollen-nectar provision, defecate, and spin a cocoon with silk-like strands. In this stage (prepupa), most individuals in a population undergo a diapause period that lasts through the winter months. Under natural conditions, *M. rotundata* complete their development through the adult stage and eclosion as ambient temperatures increase during the following spring and early summer. Under artificial commercial rearing conditions, prepupae that have received a sufficient wintering period, 8–10 mo (Richards et al. 1987), are incubated during the early summer to ensure emergence with the characteristic flush of bloom in alfalfa-seed fields in June or early July (Stephen 1981, Rank and Goerzen 1982, Richards 1984).

At most latitudes in North America, some proportion of bees in a population, especially from the first nests produced each year, will avert the late summer prepupal diapause and continue to develop through the adult stage and eclosion during the current year (Krunic 1972, Johansen and Eves 1973, Bitner 1976, Hobbs and Richards 1976, Richards 1984). From the perspective of commercial-scale alfalfa seed producers, individual bees that do not enter diapause are usually considered a loss, because it is thought that they kill diapausing nestmates during emergence (Tepedino and Frohlich 1984), and there is insufficient time and floral resources to produce and develop progeny before the onset of cooler fall temperatures. This

interesting phenomenon, commonly referred to as "second generation," has received some attention in this species, but a clear explanation of how diapause is mediated has yet to emerge (Taséi and Masure 1978, Klostermeyer 1982, Parker and Tepedino 1982, Tepedino and Parker 1986, Rank and Rank 1989).

Early work, which revealed the increased prevalence of nondiapausing individuals from the cells produced during the first half of the nesting season (Krunic 1972, Richards 1984), prompted the suggestion that total accumulated heat units over the entire summertime development period of *M. rotundata* may be a controlling factor in determining whether individuals ultimately avert diapause and emerge as adults in late summer. However, results from studies where immature *M. rotundata* were exposed to low temperatures do not support this hypothesis (Bitner 1976, Taséi and Masure 1978, Tepedino and Parker 1986). Other early work demonstrating the potential for artificial selection of populations exhibiting a high proportion of diapausing individuals (Hobbs and Richards 1976) eventually led to research which suggested that the diapausing trait in *M. rotundata* is incompletely dominant and under polygenic control (Parker 1979, Parker and Tepedino 1982, Rank and Rank 1989). The value of an effort aimed at selecting for a consistently high proportion of diapausing individuals in a population for the benefit of alfalfa seed production has been "considered to be little more than an academic exercise" because of the mixing of true-breeding populations with feral populations in commercial scale open-field situations (Hobbs and Richards 1976). Lastly, both Bitner (1976) and Parker and Tepedino (1982) suggested the possible influence of daylength on adult females and the subsequent frequency of nondiapausing individuals in their progeny, although in neither study was this hypothesis explicitly tested.

In previous work, we emphasized the connection between summertime immature development, sufficient wintering conditions, and postdiapause (the following spring) development, survival, emergence, and adult longevity (Kemp and Bosch 2000). Of particular interest is the result that elevated constant and fluctuating temperature regimes are associated with a reduction in the duration of the prepupal development stage (Kemp and Bosch 2000). Similarly, results from observations on another megachilid, the spring-emerging orchard pollinator *Osmia lignaria* Say, demonstrated shortened prepupal dormancy under fluctuating thermal conditions (Bosch and Kemp 2000, Bosch et al. 2000).

Because the prepupae of both bee species responded to changes in temperature, we decided to further investigate the effect of temperature on prepupal diapause in *M. rotundata.* Using progeny from the same maternal population described in Kemp and Bosch (2000), we exposed *M. rotundata* prepupae, reared under the same conditions from egg through cocoon completion, to differing temperature regimes from cocoon completion to emergence, and recorded development and emergence times as well as survival rates. In contrast to Kemp and Bosch (2000), nests used in this study were constructed during the second half of the nesting season, which traditionally exhibit a high proportion of diapausing bees compared with individuals from nests constructed earlier in the nesting season. This allowed for the additional comparison of the incidence of nondiapausing bees among progeny from early versus late nesting, when reared under exactly the same thermal conditions.

Materials and Methods

Bees were obtained from a population released at the beginning of June 1998 in pasture containing alfalfa near Clarkston, UT (112.0265° W longitude: 41.9135° N latitude), and managed by our laboratory (Kemp and Bosch 2000). Wood boxes with grooved polystyrene wafers and inserted paper straws (11.5 cm long, 5.5 mm diameter) were used as nesting materials. During peak nesting, a sample of newly capped paper straws were removed from the polystyrene wafers each day and taken to the Bee Biology and Systematics Laboratory (BBSL), where they were dissected. Within each nest, cells with unhatched eggs were dated assuming an approximate cell production rate of two cells per day (Klostermeyer et al. 1973, Klostermeyer 1982). Cells with hatched eggs were discarded. Female *M. rotundata* are ≈1.2–1.5 times larger than males, and female eggs are allocated larger pollen-nectar provisions, which tend to be deposited in the innermost cells of nesting cavities (Klostermeyer et al. 1973, Klostermeyer 1982). Using these criteria, the first two cells within each straw were considered females, and the last two cells males. Intermediate cells were not used, nor were nests with fewer than five cells. Bee sex was confirmed in later developmental stages (pupae and adults). Provisions with eggs were transferred to artificial clay wells (Torchio and Bosch 1992, Bosch and Kemp 2000, Kemp and Bosch 2000), which were labeled with nest number and cell position within the nest and covered with glass slide covers.

Male and female cells were assigned to various temperature treatments, so that no treatment received two cells from the same nest and sex. Sample sizes ranged between 140–150 individuals per treatment, in roughly equal numbers of males and females. Clay wells with eggs and provisions were placed in clear PVC boxes containing two additional clay wells filled with water to provide adequate humidity throughout development. All developing larvae were maintained at a constant 22°C until cocoon completion, whereupon they were transferred to (dark) temperature cabinets according to the following treatments: constant 18, 22, 26, 29, 32, and variable 14-27°C at a thermoperiod of 8:16 h (mean: 22°C). After consumption of the provision, clay blocks were checked daily and the date of cocoon completion was noted. After cocoon completion, cocoons containing prepupae were placed individually in clear gel capsules and transferred to sticky boards (20 by 25 cm boards with double-sided adhesive tape), which were x-rayed every 3 d (Stephen and Undurraga 1976). X-ray plates
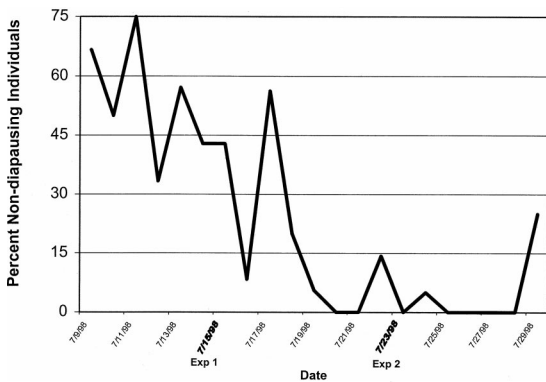
Fig. 1. Percent nondiapausing *M. rotundata* in the populations used in two experiments (Experiment 1: Kemp and Bosch (2000), Experiment 2: reported herein) reared from egg through prewintering stages at 22°C. Bold dates refer to median dates of eggs assigned to the various treatments in both experiments.

were used to record the dates when bees pupated and became adults.

Nondiapausing bees, bees that pupated during 1998, were kept in the temperature treatment to which they were assigned after cocoon completion. Cocoons were checked daily for adult emergence, whereupon they were removed from the gel capsules, individually transferred to a glass vial, held at 22°C, and monitored daily until death. Adult longevity without feeding was used as a measure of vigor (Bosch and Kemp 2000). In the case of diapausing bees, bees that did not pupate during 1998, prepupae were exposed to 3 d at 18, 14, and 10°C each before transfer to 4°C on 13 October 1998. Diapausing bees were wintered at 4°C for 213 d, after which time (14 May 1999) they were incubated at 29°C. We selected 29°C because this is the temperature at which commercial populations of *M. rotundata* are routinely incubated (Richards 1984, Murrell 1991, Kemp and Bosch 2000). After adult emergence, bees were treated in the same way as nondiapausing bees during the previous fall (1998).

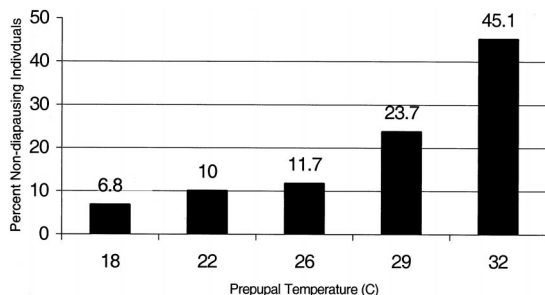We used chi-square and analysis of variance (ANOVA) procedures as appropriate to compare

Fig. 2. Percent nondiapausing *M. rotundata* in populations reared from egg through completed cocoon at 22°C, then transferred to various constant temperature treatments for the duration of prewintering.

differences among treatments, bee type (nondiapausing and diapausing bees), and sex, in selected development periods—for example, total development time (days to develop from egg to adult), emergence time (days to emerge after incubation at 29°C), and longevity (days from emergence until death at 22°C).

Results

Progeny from the constant 22°C treatment in this study, received identical temperatures from egg through prewintering as the progeny reported from the constant 22°C treatment of Kemp and Bosch (2000). However, eggs used in Kemp and Bosch (2000) were laid earlier in the season (median date 15 July 1998), whereas eggs used in the current study were laid during the latter portion of the nesting season (median date 23 July 1998) (Fig. 1). The background incidence of nondiapausing individuals was higher (34%, 41 of 121 total individuals) among the eggs used in Kemp and Bosch (2000) compared with the current study (7%, 8 of 109 individuals). Thus, in comparisons that we make herein concerning the effects of differing temperature treatments on postcocooning *M. rotundata* prepupae, we are comparing against a background incidence of 7% nondiapausing individuals at a constant 22°C.

There was a significant increase (Fig. 2) in the likelihood that *M. rotundata* prepupae would avert diapause as the constant temperatures to which they were exposed as prepupae increased from 18 to 32°C ($\chi^2 = 49.42$, df = 4, $P \le 0.001$). The incidence of prepupae averting diapause, in the only variable temperature treatment that we managed (14–27°C, mean 22°C), was similar to that from constant 22°C temperature treatment at 9.7%. Because individuals in the constant 22°C temperature treatment were reared at the same temperature from egg through the end of prewintering, our results show that fewer individuals avert diapause when cooled as prepupae than when warmed (Fig. 2).

Stage specific development intervals as well as longevity without feeding at 22°C for individuals that averted diapause are provided in Table 1. Because of small sample sizes, statistical tests were not conducted. However, the developmental stage of nondiapausing individuals apparently most affected by the transfer to various temperature regimes was the completed cocoon/pupa interval (Table 1), which appeared to lengthen with increasing constant temperatures, and to shorten with fluctuating temperatures.

For bees that entered diapause during the summer of 1998, those wintered for 213 d at 4°C and incubated at a constant 29°C the following spring (1999), we analyzed postincubation stage-specific development intervals of females and males separately because of acknowledged development differences between sexes (Kemp and Bosch 2000). When incubated at a constant 29°C during the spring of 1999, female *M. rotundata* that had been prewintered under various

Table 1. Duration (in days) of postcocooning development periods at various "prewintering" temperatures and longevity of emerged adults (in days at 22°C) for nondiapausing male and female *Megachile rotundata*

Treatment, °C	Sex	Completed cocoon/Pupa		Pupa/Adult		Adult/Emerg.		Longevity without feeding at 22°C	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
18	M	2.0	0.58	21.3	1.44	5.7	0.87	5.0	0.58
	F	None averted diapause at this temperature							
22	M	10.3	4.27	24.0	1.73	6.8	1.50	2.8	0.48
	F	7.8	1.75	27.0	1.23	6.3	0.95	3.0	0.00
26	M	9.3	2.93	21.4	1.52	6.9	0.81	3.9	1.03
	F	None averted diapause at this temperature							
29	M	13.5	3.42	21.4	1.10	5.3	0.41	4.4	0.46
	F	16.5	8.77	27.8	0.75	5.8	1.32	3.0	0.82
32	M	28.2	3.34	22.6	0.74	7.3	0.46	3.1	0.20
	F	24.7	4.34	26.2	0.96	6.0	0.68	2.8	0.69
14–27 (mean 22)	M	6.5	1.40	25.3	0.90	4.8	0.59	3.3	0.62
	F	7.0	1.00	25.3	0.88	6.3	0.88	3.0	0.58

temperature regimes, required significantly different periods of time to emerge ($F = 11.99$, df = 5, $P < 0.0001$), ranging between 29 and 32 d. Means separation ($\alpha = 0.05$) with Tukey's Studentized Range honestly significant difference (HSD) revealed that females prewintered at the variable 14–27°C and constant 18°C treatments generally required less time to emerge and constituted most of the observed variation in emergence times (Table 2). There were also significant differences in incubation (at a constant 29°C) to emergence intervals ($F = 8.70$, df = 5, $P < 0.0001$) among males, ranging from 27 d for individuals prewintered under the variable 14–27°C regime to 30 d for individuals prewintered at a constant 26°C. For both diapausing males and females, the adult/emergence interval was ⅓–½ the duration of the incubation/pupa or pupa/adult intervals, respectively, regardless of the prewintering temperature regimes to which they were exposed (Table 2).

There were no significant differences in longevity, without feeding at constant 22°C, among diapausing male *M. rotundata* ($F = 2.08$, df = 5, $P > 0.06$) prewintered under the various temperature regimes (Table 3). Similarly, although there were significant differences in longevity among diapausing females ($F = 2.75$, df = 5, $P < 0.02$), a Tukey's studentized range honestly significant difference (HSD) means separa-

tion test revealed only one significant difference ($\alpha = 0.05$), that individuals lived longer (6 d) when prewintered at a constant 22°C than when prewintered at a variable 14–27°C (4 d, Table 3).

There were no significant differences in prepupal mortality levels among individuals reared from eggs through completed cocoon at constant 22°C and then transferred to the various prewintering temperature regimes (Table 4, $\chi^2 = 10.25$, df = 5, $P = 0.07$). Among individuals exhibiting diapause, there were significant differences in pupal ($\chi^2 = 34.79$, df = 5, $P \leq 0.001$) and late developmental ($\chi^2 = 25.30$, df = 5, $P \leq 0.001$) mortality among individuals exposed to the various prewintering treatments (Table 4). For diapausing individuals, pupal mortality was highest among those prewintered at a constant 26°C and lowest among individuals prewintered at a constant 32°C (Table 4). Late developmental mortality was highest among those prewintered at a constant 26°C and a variable 14:27°C, and lowest when prewintered at 22°C (Table 4). Over the entire life cycle, *M. rotundata* exhibited the lowest mortality (25%) when prewintered at the same temperature under which they developed from egg through completed cocoon, constant 22°C, and highest when prewintered at a constant 26°C ($\chi^2 = 38.44$, df = 5, $P \leq 0.0001$).

Table 2. Duration (in days) of postwintering development periods at constant 29°C for diapausing male and female *Megachile rotundata* prewintered (from completed cocoon to start of winter storage) under differing temperature regimes

Treatment, °C	Sex	Incubation at 29°C/Pupa		Pupa/Adult		Adult/Emerg.		Incubation at 29°C/Emerg.	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
18	M	13.5	0.42	11.0	0.27	3.9	0.18	28.5	0.30
	F	13.3	0.27	11.4	0.20	5.1	0.18	29.7	0.19
22	M	13.9	0.41	10.8	0.21	4.1	0.14	28.8	0.28
	F	16.3	0.33	11.0	0.24	4.3	0.21	31.6	0.20
26	M	15.9	0.80	9.9	0.32	4.6	0.22	30.4	0.65
	F	14.1	0.58	11.4	0.42	5.0	0.32	30.5	0.48
29	M	12.6	0.48	11.6	0.24	3.8	0.21	28.0	0.38
	F	14.2	0.36	11.5	0.30	4.8	0.30	30.5	0.25
32	M	11.9	0.42	11.9	0.12	3.8	0.24	27.6	0.36
	F	15.1	0.64	12.2	0.30	4.0	0.28	31.4	0.51
14–27 (mean 22)	M	10.9	0.52	12.3	0.24	3.5	0.21	26.7	0.37
	F	12.4	0.23	11.8	0.23	4.9	0.18	29.2	0.21

Table 3. Longevity without feeding (in days at 22°C) for diapausing male and female *Megachile rotundata* which were reared under various prewintering temperatures, were wintered at 4°C, and incubated at 29°C

Treatment, °C	Sex	Longevity without feeding Mean	Longevity without feeding SE	Range, d
18	M	5.0	0.39	10
	F	5.0	0.39	10
22	M	6.3	0.53	12
	F	6.2	0.43	12
26	M	4.7	0.51	12
	F	4.7	0.52	9
29	M	5.3	0.44	11
	F	4.7	0.59	10
32	M	5.5	0.55	11
	F	4.7	0.59	11
14–27	M	4.9	0.40	10
(mean 22)	F	4.0	0.45	9

Discussion

Prewintering Temperatures. Despite the statistical differences in development and longevity that we detected among diapausing *M. rotundata* populations exposed to various prewintering regimes, the ranges were not great. Male *M. rotundata* required 27–30 d to transit from prepupae to emergence as adults at constant 29°C, whereas females required slightly more time, between 29 and 32 d (Table 2). These ranges are similar to previous reports under different treatment conditions (Richards et al. 1987, Richards and Whitfield 1988, Murrell 1991, Kemp and Bosch 2000). Likewise, longevity among diapausing *M. rotundata* populations exposed to the various temperature regimes that we maintained ranged from 5 to 6 d for males and 4 to 6 d for females (Table 3).

Mortality among diapausing populations in this investigation, which differed from that in our previous investigations (Kemp and Bosch 2000), was lower for low temperature treatments and higher among the high temperature treatments. This may have been due in part to the rearing of all developing eggs and larvae at a cool constant 22°C through the completed cocoon stage. Recent results obtained with the orchard pollinator *O. lignaria* (Bosch et al. 2000), which prewinters and winters as an adult instead of the prepupal stage as in *M. rotundata*, revealed that extended periods of high prewintering temperatures resulted in apparent body fat consumption and reductions in adult longevity the following spring. Although the

elevated prewintering temperatures that we subjected *M. rotundata* to did not have negative impacts on longevity the following spring, they had considerable impact on the likelihood with which individuals averted diapause and emerged during the current year (Fig. 2).

Diapause. The most obvious result of different prewintering thermal conditions was the observed elevated levels of nondiapausing forms at higher temperatures (Fig. 2). Notwithstanding the influence of other factors (see below), this result indicates that the prepupal stage of *M. rotundata* (specifically, of individuals from cells constructed during the second half of the nesting season) is sensitive to external temperature cues. This result contrasts with previous investigations that suggest that the fate (nondiapausing versus diapausing) of *M. rotundata* immatures is fixed from the early developmental stages.

As we seek to better understand the frequency of diapause in *M. rotundata* populations, as well as the factors that influence its prevalence, it is important to consider contributions made by genetic variability and phenotype plasticity (Nijhout 1999, Tammaru et al. 1999). Previous investigations (Hobbs and Richards 1976, Parker 1979, Parker and Tepedino 1982, Rank and Rank 1989), which explored the prevalence of diapause in geographically separate populations, clearly demonstrated that diapause is incompletely dominant and is under polygenic control. Genetic control is also indicated by the fact that individuals within nests are normally predominantly either nondiapause or diapause forms, rather than a mixture of the two (Krunic 1972, Johansen and Eves 1973). Parker and Tepedino (1982) also acknowledged the likelihood that a decrease in daylength below some critical level may in turn influence the prevalence of diapausing individuals produced, due primarily to maternal control as has been demonstrated in other Hymenoptera (Ryan 1965, Parrish and Davis 1978). If true, then variability in the proportion of *M. rotundata* exhibiting diapause in a given year would be, in part, related to the geographic origin of the maternal population, the location of the study site, and the time of the season during which bees were nesting (for example, before or after the summer solstice at northerly latitudes).

Previous observations (Krunic 1972; Johansen and Eves 1973; Bitner 1976; Hobbs and Richards 1976; Richards 1984; Tepedino and Parker 1986, 1988), as

Table 4. Sample sizes and mortality for male and female *M. rotundata* prewintered under differing temperature regimes

Treatment, °C	n	Prepupal mortality	Pupal mortality Nondiapausing (1-y) forms	Pupal mortality Diapausing (2-y) forms	Late developmental mortality Nondiapausing (1-y) forms	Late developmental mortality Diapausing (2-y) forms	Total mortality
18	144	13 (9%)	4 (3%)	13 (10%)	2 (2%)	17 (15%)	49 (34%)
22	145	15 (10%)	5 (4%)	7 (6%)	0 (0%)	9 (8%)	36 (25%)
26	149	25 (17%)	6 (5%)	29 (25%)	1 (1%)	26 (30%)	87 (58%)
29	144	13 (9%)	8 (6%)	13 (11%)	6 (5%)	19 (18%)	59 (43%)
32	143	11 (8%)	13 (10%)	3 (3%)	15 (13%)	20 (20%)	62 (43%)
14–27 (mean 22)	144	9 (6%)	2 (1%)	18 (14%)	0 (0%)	33 (29%)	62 (43%)

well as our own, showing a seasonal decline in the prevalence in nondiapausing individuals in a population (Fig. 1) provide support for the hypothesis suggested by Parker and Tepedino (1982) that at least part of the variability in observed diapause prevalence each year in *M. rotundata* populations is due to day-length exposures of nesting females. To this variability we must also add the apparent phenotypic plasticity exhibited by current season offspring which, when exposed to increasing prewintering (postcompleted cocoon) temperatures, will avert diapause in ever increasing proportions (Fig. 2). Because nests assigned to the 22°C treatments from both this and our previous study (Kemp and Bosch 2000) were exposed to the same temperature conditions from the egg through completed cocoon stage, our results seriously undermine the commonly held hypothesis that increases in the frequency of nondiapausing individuals in a population of *M. rotundata* are due to the overall accumulation of heat units during that period.

The combined influence of maternal effects triggered by photoperiod and current year generation phenotypic plasticity can result in significant pollinator losses for next year's crop, through a high prevalence of nondiapausing forms, none of which will survive until the following spring. The chronically high levels of nondiapausing forms in *M. rotundata* populations observed in California (Peterson, personal communication) are likely to be, in part, a result of nesting seasons that are completed entirely under shorter, but increasing, daylengths than those of more northerly alfalfa seed-production areas. Exposure of prepupae to high temperatures, either ambient or resulting from heat retention in certain types of nesting materials (Peterson et al. 1994) after the completed cocoon stage, would only exacerbate the problem of elevated proportions of nondiapausing individuals, and result in greater losses to the pollinator population for the following spring. Exposing postcocooning bees to cooler temperatures will not only result in lower frequencies of individuals averting diapause, but will reduce late mortality among diapausing individuals as well.

Although alfalfa seed producers can presently do little about the contribution of genetic variability and phenotypic plasticity of the maternal generation, because the timing of alfalfa bloom is optimized according to plant production factors rather than bee reproduction, they do have some control over the thermal environment of this year's prepupae. Producers seeking to reduce the exposure of prepupae to elevated temperatures, such as those frequently encountered in the Central Valley of California, by using thermally superior nesting materials (Peterson et al. 1994) as well as removing them from the field in a timely fashion, will likely be rewarded with fewer nondiapausing individuals in their *M. rotundata* populations.

Acknowledgments

References Cited

Bitner, R. M. 1976. Ecological management of the alfalfa leafcutter bee, *Megachile pacifica* (Panzer), with emphasis on diapause induction. Ph.D. Dissertation, Department of Biology, Utah State University, Logan, UT.

Bosch, J., and W. P. Kemp. 2000. Development and emergence of the orchard pollinator, *Osmia lignaria* (Hymenoptera: Megachilidae). Environ. Entomol. 29: 8–13.

Bosch, J., W. P. Kemp, and S. Peterson. 2000. Management of *Osmia lignaria* (Hymenoptera: Megachilidae) populations for almond pollination: Methods to advance bee emergence. Environ. Entomol. 29: 874–883.

Hobbs, G. A., and K. W. Richards. 1976. Selection for a univoltine strain of *Megachile* (*Eutricharaea*) *pacifica* (Hymenoptera: Megachilidae). Can. Entomol. 108: 165–167.

Johansen, C. A., and J. D. Eves. 1973. Effect of chilling, humidity and seasonal conditions on emergence of the alfalfa leafcutting bee. Environ. Entomol. 2: 23–26.

Kemp, W. P., and J. Bosch. 2000. Development and emergence of the alfalfa pollinator, *Megachile rotundata* (Hymenoptera: Megachilidae). Ann. Entomol. Soc. Am. 93: 904–911.

Klostermeyer, E. C. 1982. Biology of the alfalfa leafcutting bee, pp. 10–19. *In* G. H. Rank [ed.], Proceedings, First International Symposium on Alfalfa Leafcutting Bee Management. University of Saskatchewan, Saskatoon.

Klostermeyer, E. C., J. S. Mech, Jr., and W. B. Rasmussen. 1973. Sex and weight of *Megachile rotundata* (Hymenoptera: Megachilidae) progeny associated with provision weights. J. Kans. Entomol. Soc. 46: 536–548.

Krombein, K. V. 1948. An adventive *Megachile* in Washington, DC. (Hymenoptera: Megachilidae). Proc. Entomol. Soc. Wash. 50: 14.

Krunic, M. D. 1972. Voltinism in *Megachile rotundata* (Hymenoptera: Megachilidae) in southern Canada. Can. Entomol. 104: 185–188.

Krunic, M. D., and C. F. Hinks. 1972. The effect of temperature and of temperature pretreatment on diapause and on the synchronization of adult emergence in *Megachile rotundata.* Can. Entomol. 104: 889–893.

Murrell, D. 1991. A calendar of incubation for alfalfa leafcutting bees. Sask. Agric. Newsl. 13.

Nijhout, H. F. 1999. Control mechanisms of polyphenic development in insects. BioScience 49: 181–192.

Parker, F. D. 1979. Alfalfa leafcutter bee: Origin of female and its influence on diapause. Proceedings, IVth International Symposium on Pollination. Md. Agric. Exp. Stn. Spec. Misc. Publ. 1: 269–272.

Parker, F. D., and V. J. Tepedino. 1982. Maternal influence on diapause in the alfalfa leafcutting bee (Hymenoptera: Megachilidae). Ann. Entomol. Soc. Am. 75: 407–410.

Parrish, D. S., and D. W. Davis. 1978. Inhibition of diapause in *Bathyplectes curculionis*, a parasite of the alfalfa weevil. Ann. Entomol. Soc. Am. 71: 103–107.

Peterson, S. S., C. R. Baird, and R. M. Bitner. 1992. Current status of the alfalfa leafcutting bee, *Megachile rotundata*, as a pollinator of alfalfa seed. Bee Sci. 2: 135–142.

Peterson, S. S., C. R. Baird, and R. M. Bitner. 1994. Heat retention during incubation in nests of the alfalfa leafcutting bee (Hymenoptera: Megachilidae). J. Econ. Entomol. 87: 345–349.

Rank, G. H., and D. W. Goerzen. 1982. Shelter design and hive placement for optimizing alfalfa leafcutter bee ac-

tivity, pp. 144–151. *In* G. H. Rank [ed.], Proceedings, First International Symposium on Alfalfa Leafcutting Bee Management. University of Saskatchewan, Saskatoon.

Rank, G. H., and F. P. Rank. 1989. Diapause intensity in a French univoltine and a Saskatchewan commercial strain of *Megachile rotundata* (Fab.). Can. Entomol. 121: 141–148.

Richards, K. W. 1984. Alfalfa leafcutter bee management in Western Canada. Agriculture Canada Publication 1495/E. Agriculture Canada, Ottawa.

Richards, K. W., and G. H. Whitfield. 1988. Emergence and survival of leafcutter bees, *Megachile rotundata*, held at constant incubation temperatures (Hymenoptera: Megachilidae). J. Apic. Res. 27: 197–204.

Richards, K. W., G. H. Whitfield, and G. B. Schaalje. 1987. Effects of temperature and duration of winter storage on survival and period of emergence for the alfalfa leafcutter bee (Hymenoptera: Megachilidae). J. Kansas Entomol. Soc. 60: 70–76.

Ryan, R. B. 1965. Maternal influence on diapause in a parasitic insect, *Coeloides brunneri* Vier (Hymenoptera: Braconidae). J. Insect Physiol. 11: 1331–1336.

Stephen, W. P. 1981. The design and function of field domiciles and incubators for leafcutting bee management (*Megachile rotundata* (Fabricius)). Bulletin 654. Oregon State University, Agricultural Experiment Station, Corvallis, OR.

Stephen, W. P., and C. E. Osgood. 1965. Influence of tunnel size and nesting medium on sex ratios in a leaf-cutter bee, *Megachile rotundata.* J. Econ. Entomol. 58: 965–968.

Stephen, W. P., and J. Undurraga. 1976. X-Radiography, an analytical tool in population studies of the leafcutter bee, *Megachile pacifica.* J. Apic. Res. 15: 81–87.

Tammaru, T., K. Ruohamäki, and I. Saloniemi. 1999. Within-season variability of pupal period in the autumnal moth: a bet-hedging strategy? Ecology 80: 1666–1677.

Taséi, J. N., and M. M. Masure. 1978. Sur quelques facteurs influencant le development de *Megachile pacifica* Panz. (Hymenoptera: Megachilidae). Apidologie 9: 273–290.

Tepedino, V. J., and D. R. Frohlich. 1984. Fratricide in *Megachile rotundata*, a non-social megachilid bee: impartial treatment of sibs and non-sibs. Behav. Ecol. Sociobiol. 15: 19–23.

Tepedino, V. J., and F. D. Parker. 1986. Effect of rearing temperature on mortality, second-generation emergence, and size of adult in *Megachile rotundata* (Hymenoptera: Megachilidae). J. Econ. Entomol. 79: 974–977.

Tepedino, V. J., and F. D. Parker. 1988. Alteration of sex ratio in a partially bivoltine bee, *Megachile rotundata* (Hymenoptera: Megachilidae). Ann. Entomol. Soc. Am. 81: 467–476.

Torchio, P. F., and J. Bosch. 1992. Biology of *Tricrania stansburyi*, a meloid beetle cleptoparasite of the bee *Osmia lignaria propinqua* (Hymenoptera: Megachilidae) Ann. Entomol. Soc. Am. 85: 713–721.

Undurraga, J. M. 1978. Effects of temperature and other abiotic factors on development and survival of the immature stages of the alfalfa leafcutting bee, *Megachile pacifica* (Panzer) = *rotundata* (F.) (Hymenoptera: Megachilidae). Ph.D. Dissertation, Dep. of Biology, Utah State University, Logan, UT.

Whitfield, G. H., and K. W. Richards. 1992. Temperature-dependent development and survival of immature stages of the alfalfa leafcutter bee, *Megachile rotundata* (Hymenoptera: Megachilidae). Apidologie 23: 11–23.